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A NEW SPECIES OF THE AETOSAUR *TYPOTHORAX* (ARCHOSAURIA:STAGONOLEPIDIDAE) FROM THE UPPER TRIASSIC OF EAST-CENTRAL NEW MEXICO

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Abstract—We describe an incomplete skeleton of a new species of the aetosaur *Typothorax*, *T. antiquum*, from the Los Esteros Member of the Santa Rosa Formation near Lamy, Santa Fe County, New Mexico. Features that diagnose *T. antiquum* from the type and only other species of *Typothorax*, *T. coccinarum* Cope, are the relatively narrow paramedian scutes (width: length ratio ~2-3), coarser and less dense pitting on the dorsal paramedian scutes, more pronounced radial ridges on the dorsal lateral scutes, and a more robust ilium, with more prominent and thicker peduncles, lateral buttress and iliac blade. We also refer incomplete scutes and scute fragments from the Garita Creek Formation in east-central New Mexico to *T. antiquum*. *Typothorax* scutes from the overlying Trujillo Formation in east-central New Mexico pertain to *T. coccinarum* and are the stratigraphically lowest occurrence (LO) of that taxon. The LO of *T. antiquum* is older (Adamanian: latest Carnian) than the LO of the much more common *T. coccinarum* (Revueltian: early-mid Norian). *T. antiquum* is a relatively rare Adamanian aetosaur and thus has limited biochronological utility. The morphology and temporal distribution of *Typothorax* species suggests they represent a single, anagenetic lineage, with *T. antiquum* directly ancestral to *T. coccinarum*.

Keywords: aetosaur, *Typothorax*, Triassic, Chinle Group, New Mexico, Revueltian, Adamanian.

INTRODUCTION

One of the first Late Triassic tetrapods to be described from the American Southwest was the aetosaur *Typothorax coccinarum*. Cope (1875) named the species for fragments of dermal armor he collected from the upper part of the Chinle Group near Gallina, Rio Arriba County, New Mexico (Lucas and Hunt, 1992; see also Heckert and Lucas, 2002a; Lucas et al., 2002). Since that time, numerous specimens of *T. coccinarum* have been collected from upper Chinle strata in New Mexico and Arizona (e.g., Long and Ballew, 1985; Hunt et al., 1993; Long and Murry, 1995; Heckert and Lucas, 2000, 2002a; Hunt, 2001b). Indeed, *T. coccinarum* is one of the most common tetrapod fossils found in strata of the upper Chinle Group. Its first appearance and stratigraphic range have also been used to define the Revueltian land-vertebrate faunachron (Lucas and Hunt, 1993; Lucas, 1998).

Typothorax, however, has been reported from Chinle Group strata that are older than Revueltian (Figs. 1-2). These include fragmentary scutes from the Adamanian Garita Creek Formation in east-central New Mexico (Hunt and Lucas, 1989, 1993). Subsequently, Hunt and Lucas (1995) mentioned the incomplete skeleton of a "new aetosaur" similar to *Typothorax* from the Tres Lagunas Member of the Santa Rosa Formation near Lamy in Santa Fe County, New Mexico (Figs. 1-2). Long and Murry (1995, p. 234) also listed specimens they referred to *T. coccinarum* from the Garita Creek Formation. These older fossils, however, do not belong to *T. coccinarum*, but instead pertain to a new species of *Typothorax* described here. Thus, in this paper we describe a new species of *Typothorax*, discuss the first appearance datum (FAD) of *T. coccinarum*, and comment on the biostratigraphic and biochronologic significance of the genus as well as its evoluton.

Institutional abbreviations: MDM = Mesalands Dinosaur Museum, Tucumcari, New Mexico; NMMNH = New Mexico Museum of Natural History, Albuquerque; UCMP = University of California Museum of Paleontology, Berkeley.

SYSTEMATIC PALEONTOLOGY

Superorder ARCHOSAURIA Cope, 1869
Order CROCODYLOTARSI Benton and Clark, 1988
Suborder AETOSAURIA Nicholson and Lydekker, 1889
Family STAGONOLEPIDIDAE Lydekker, 1887
Subfamily DESMATOSUCHINAE Huene, 1942
Genus *Typothorax* Cope, 1875
***Typothorax antiquum*, new species**
(Figures 3-9, 10A, E-G)
(Tables 1-6)

1989 *Typothorax* sp.: Hunt et al., p. 65, fig. 3c.
1995 new aetosaur 3: Hunt and Lucas, p. 244.
1995 *Typothorax coccinarum*: Hunt and Lucas, fig. 2k .
1995 *Typothorax coccinarum* (in part): Long and Murry, p. 234.

Holotype: NMMNH P-36075, an incomplete skeleton consisting of a partial carapace, cervical, dorsal, sacral, and caudal vertebrae, part of a left scapulocoracoid, humerus, radius and ulna, both ilia and ischia, femora, tibiae, fibulae, astragali and calcanea, and many metapodials, podials, and phalanges (Figs. 3-9).

Type horizon and locality: Tres Lagunas Member of the Santa Rosa Formation (Fig. 2) at NMMNH locality 3108, UTM zone 13, 421750E, 3925320N, NAD 27, Santa Fe County, New Mexico.

Referred specimens: Referred specimens of *Typothorax antiquum* from the Garita Creek Formation in east-central New Mexico are: NMMNH P-3674, seven paramedian scute fragments from NMMNH locality 410 (Hunt et al., 1989, fig. 3c); P-3679, fragment of a dorsal paramedian scute from locality 404; P-17508, five paramedian scute fragments from locality 426; P-17554, two paramedian scute fragments from locality 411; P-17569 (Fig. 10E), three paramedian scute fragments from locality 413; P-17579 (Fig. 10F-G), a lateral scute fragment from locality 404; P-17581, two para-

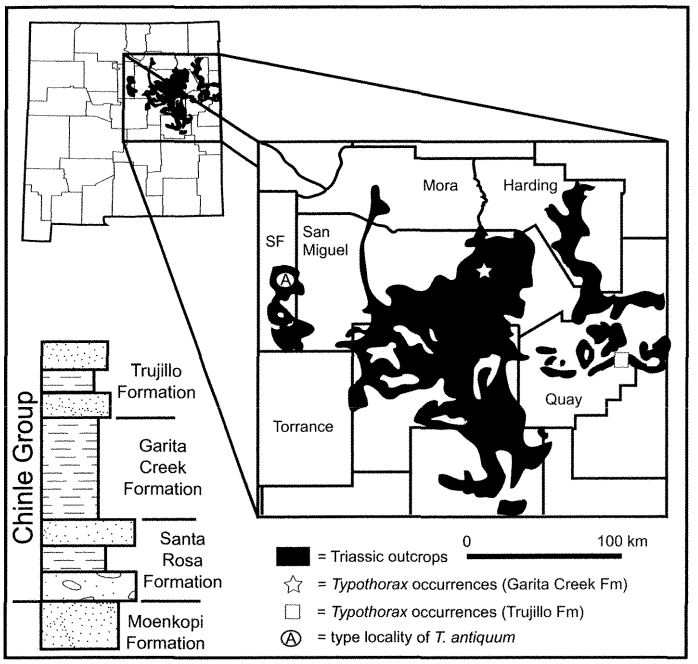

FIGURE 1. Outcrop map and generalized stratigraphic section (after Lucas, 1991) of east-central New Mexico showing localities of *Typothorax* specimens documented in this paper.

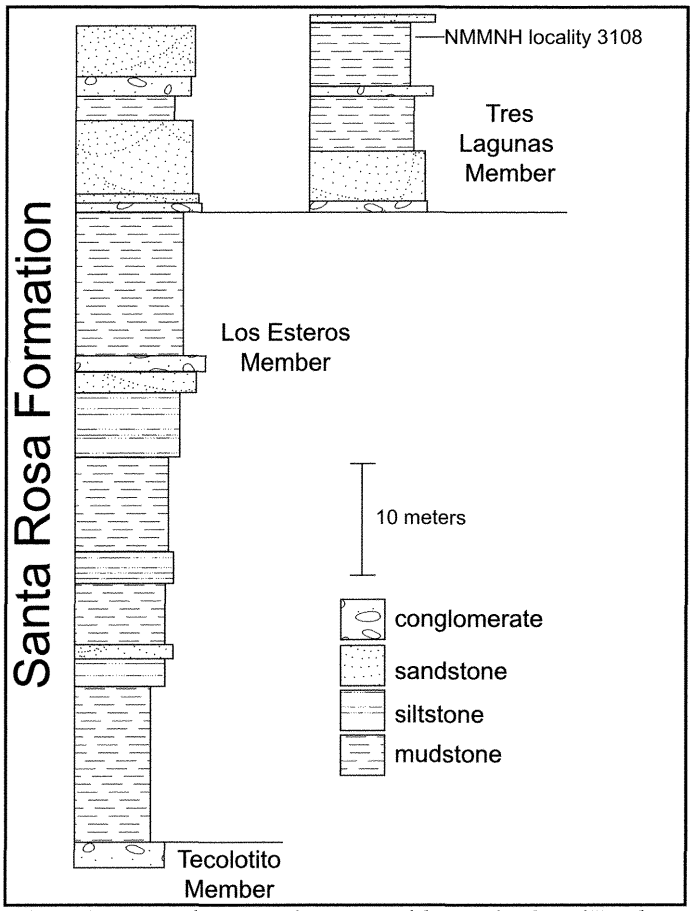

FIGURE 2. Measured stratigraphic section of the type locality of *Typothorax antiquum*.

median scute fragments from locality 401; P-17587, a paramedian scute fragment from locality 415; and P-17880 (Hunt and Lucas, 1995, fig. 2k; Fig. 10A), a partial paramedian scute from locality 1178. Note that Hunt and Lucas (1995, p. 246) indicated that P-17880 was from the Garita Creek Formation *contra* Long and Murry (1995, p. 234), who indicated that this specimen was from the Tres Lagunas Member of the Santa Rosa Formation.

Etymology: *Antiquus* (Latin) for "old," indicating the older age of *T. antiquum* relative to *T. coccinarum*.

Diagnosis: A species of *Typothorax* distinguished from *T. coccinarum* by its relatively narrow paramedian scutes (width: length ratio ~2-3), coarser and less dense pitting on the dorsal paramedian scutes, more pronounced radial ridges on the dorsal lateral scutes, and a more robust ilium, with more prominent and thicker peduncles, lateral buttress and iliac blade.

Description: Here, we describe in detail NMMNH P-36075, the holotype of *T. antiquum*. Measurements are in Tables 1-6. We illustrate three of the 10 cervical(?) scutes (Fig. 3A-C). These can be classed as those that are wider than long, and thus paramedians (two scutes), and those that are longer than wide (eight scutes), which are probably ventral scutes (Table 1). All are slightly convex dorsally, lack spikes, have anterior bars, and have the same kind of round, shallow pits and raised ridges that ornament the paramedian scutes. Dorsal bosses are weak to nonexistent.

We illustrate six dorsal paramedian scutes (Figs. 3D-G, 4A-B, E-G), and at least 20 more are preserved, varying from fragments to complete scutes. These scutes are broad (width:length > 2.5:1, see Table 2) with an ornamentation consisting of pits randomly distributed across the dorsal surface and prominent ventral keels that extend across the entire width of the scute. They thus resemble the scutes of *T. coccinarum* (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000), but are markedly different in being relatively narrow; the width:length ratios of the widest scutes of *T. coccinarum* are 4.0, but in *T. antiquum* this ratio is always 3:1 (T able 2). In general, the pits on the dorsal surfaces of the scutes of *T. antiquum* are shallower and less dense than are those of *T. coccinarum*, though there may be some overlap in this feature. The scutes of *Typothorax* lack the ventral flexure typical of *Redondasuchus* scutes, which are otherwise superficially similar. These scutes lack dorsal bosses, but the pits radiate from a point medial to the center of the posterior margin of the scute, which is typical of most aetosaurs, except *Desmatosuchus* and *T. coccinarum*.

There are 16 lateral scutes, but most are damaged (Table 3). The lateral scute illustrated here (Fig. 4H-I) generally resembles the lateral scutes of *T. coccinarum* (Long and Ballew, 1985, fig. 10), but it differs in its more pronounced radial ridges and broader, shallower and less numerous pits. Indeed, this scute is strikingly similar to lateral scutes assigned to *Paratypothorax* by Long and Murry (1995, fig. 114F-G) but lacks the well-developed spike. In other respects, including their acute flexure, dorsal flanges that are less wide than the lateral flanges and a backward-pointing projection or weakly developed spike, these scutes are essentially identical to those of *T. coccinarum*.

There are four caudal scutes, one of which is illustrated (Fig. 4C-D). All are square to rectangular with a posterior boss offset slightly toward the midline. The texture of the pitting is the same as in the dorsal paramedian scutes. As is typical in aetosaurs, the dorsal boss is best developed in the caudal scutes. Indeed, only the posterior dorsal and caudal paramedians of *T. coccinarum* bear bosses, and this appears to be true of *T. antiquum* as well.

There are 16 nearly complete vertebrae, of which we illustrate two, one dorsal and one caudal (Fig. 5A-D). All are amphicoelous. One dorsal centrum (Fig. 5A-B) is relatively broad, with an anterior articular face that is wider than tall. The posterior articular face is similarly wide. The neural arch and spine are approximately twice as tall as the centrum. As is typical in aetosaurs and some other basal archosaurs, the neural spine is expanded

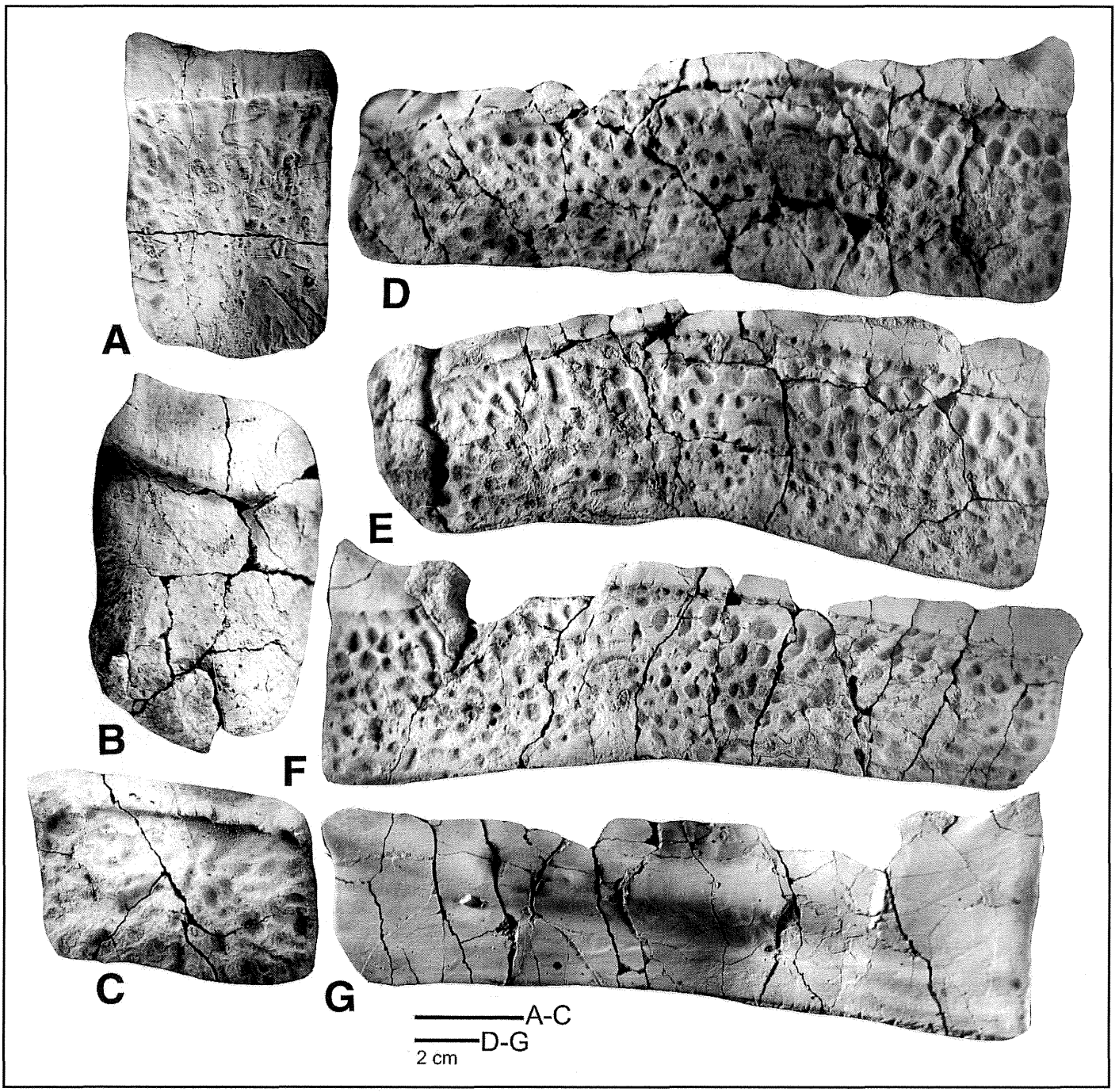

FIGURE 3. Selected dorsal scutes of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-B**, Cervical scute in **A**, dorsal and **B**, ventral views. **C**, Cervical scute in dorsal view. **D-G**, Paramedian plates in **D-F**, dorsal and **G**, ventral views.

distally, presumably to help support the carapace. The transverse processes are elongate and, unusually, directed slightly ventrally. Although not well preserved, they are moderately long, approximately 1.5 times as long as the centrum is high.

The illustrated caudal vertebra (Fig. 5C-D) is similarly broad, but with a proportionately lower neural spine. The neural spine is transversely expanded distally, much more so than in the other vertebrae. The transverse processes are particularly striking, and extend dorsally and laterally for approximately twice the width of the centrum on each side. They are so long and project so far dorsally that they almost surely helped to support the carapace, as they are even higher than the neural spine.

The gastralia (e.g., Fig. 5E-F) are typical of basal archosaurs,

TABLE 1. Measurements of cervical scutes of NMMNH P-36075, holotype of *T. antiquum* (in mm).

cervical dorsals	length	width	cervical ventrals?	length	width
1	52	112	1	54	35
2	34	62	2	59	39
3	34	49	3	63	41
			4	41+	39
			5	40+	36
			6	40	32
			7	49	39
			8	50	30+

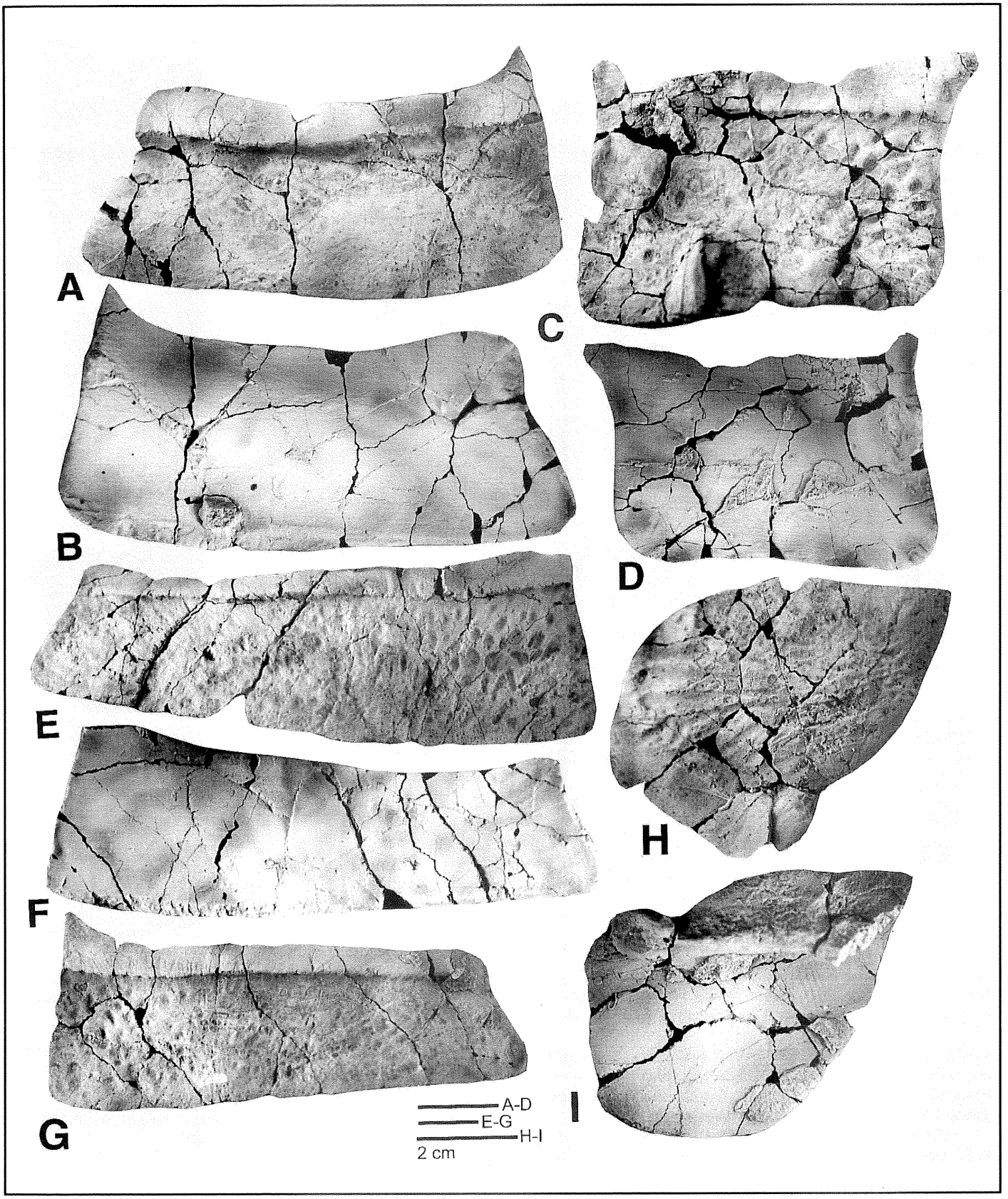

FIGURE 4. Selected scutes of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-B**, **E-G**, Dorsal paramedian scutes in dorsal (A, E, G) and ventral (B, F) views. **C-D**, Dorsal caudal scute in **C**, dorsal and **D**, ventral views. **H-I**, Lateral scute in **H**, dorsal and **I**, ventral views.

TABLE 2. Measurements of dorsal paramedian scutes of NMMNH P-36075, holotype of *T. antiquum* (in mm).

side	length	width	W:L
left	84	216	2.6
left	75	210	2.8
left	66	187	2.8
left	53	104	2.0
right	79	225	2.8
right	72	155	2.2
right	68±	212	3.1
right	75	155+	x
right	66	186	2.8
right	81	145+	x
right	79	222	2.8
right	73	188+	x
right	70	165+	x
left	66	157+	2.4
left	57	136	2.4
left	63	144+	x
left	75	176+	x

TABLE 3. Measurements of lateral and caudal scutes of NMMNH P-36075, holotype of *T. antiquum* (in mm).

Lateral scutes		
scute	**length**	**width**
1	50	72
2	45	69
3	38	63
4	broken	68
5	52	70
6	35	62
7	40	60
8	51	78
9	48	68
10	48	65
Caudal scutes		
scute	**length**	**width**
1 (11?)	55	90
2 (12?)	50	128±
3 (13?)	54	81±

TABLE 4. Measurements of vertebrae of NMMNH P-36075, holotype of *T. antiquum*.

thoracic centra	**max. ant. diameter**	**max. post. diameter**	**length**
A	25	25	26
B	26	x	34
C	24	24	23
D	28	28	40
E	24	x	23
F	32	30	38
G	27	29	39
dorsal centra	**max. ant. diameter**	**max. post. diameter**	**length**
A	35	35	30
B	31	31	30
C	31	30	40
D	39	38	51
E	39	41	36
F	34	34	31
caudal centra	**max. ant. diameter**	**max. post. diameter**	**length**
A	30	30	51
B	24	25	46

with a broad curve forming an oblique (~150°) angle. The dorsal (interior) surface is narrower but more rounded than the broad, flat ventral (exterior) surface.

The nearly complete pelvis (Fig. 6) consists of both ilia, ischia, and two sacral vertebrae, all fused into a single element. No pubes are preserved. The two sacral vertebrae are amphicoelous, and their centra are hour-glass shaped: tightly constricted in the midline. Their articular surfaces are substantially wider than tall. The anterior and posterior zygopophyses are relatively small, short and transversely broad. The neural spines are low, and their dorsal edges are laterally expanded flanges that form a platform to support the armor. The transverse processes are long and widen significantly to attach to the auricular edges of the ilia.

The ilium has a large blade that forms a nearly flat platform in the horizontal plane that overhangs the acetabulum. This platform has a sinuous and thickened lateral edge and a flat-to-slightly-concave dorsal surface. Its ventral surface is divided by a strong buttress (ridge) that rises above the acetabular portion of the ilium closer to the pubic than to the ischial peduncle. The antero-ventral surface of the iliac blade is a laterally broad concave surface anterior to the buttress (anterior blade) and a smaller, antero-posteriorly oriented concavity posterior to the buttress (posterior blade). The anterior blade is relatively weak, and does not project nearly as far as is typical of *T. coccinarum* (e.g., Long and Murry, 1995, figs. 106-107), or even most other aetosaurs (Long and Murry, 1995; Heckert and Lucas, 2000). The posterior blade forms a broad flange and is rounded postero-dorsally.

The ilium forms most of the acetabulum. Its pubic peduncle is thick and antero-laterally convex. The articular surface for the pubis is flat. The articular surface for the ischium is more v-shaped, the opening of the "v" pointing postero-ventrally. The acetabulum is a deep, round fossa that is well buttressed anteriorly and dorsally. The ilium differs from that of *T. coccinarum* (Long and Murry, 1995, fig. 106-107) in being more robust, with more prominent and thicker peduncles, lateral buttress and iliac blade, particularly the posterior projection of the blade. The result is an ilium that is more similar to that of other aetosaurs than *T. coccinarum* in lacking a pronounced constriction between the acetabular rim and the dorsal margin. As in other aetosaurs, the acetabulum is directed ventrally, which suggests that aetosaurs may have had a more erect limb posture than attributed to them by Parrish (1986).

The ischial portion of the acetabulum is relatively shallow, though the acetabular rim portion of the ischium is well defined. Ventrally, the ischium continues as a posteriorly swept back, ventro-laterally convex blade. The two blades fuse ventrally; the anterior half of their fusion is a prominent, thick flange; posteriorly the line of fusion is an open suture that divides a posteriorly projecting horizontal plate of bone.

Only the distal piece of the left scapulocoracoid is preserved, and it is no different from that of *Typothorax coccinarum* illustrated by Long and Murry (1995, fig. 105A-B). The glenoid fossa is shallow and imperforate, as in *T. coccinarum* and unlike *Desmatosuchus* and *Stagonolepis* (cf. Long and Murry, 1995). The sub-glenoid pillar is prominent and well developed.

The humerus is a stout bone with a rounded proximal end, a constricted ovoid (dorso-ventrally flattened) shaft and a flaring distal end. This bone has a nearly round, thick proximal end that flares out slightly from the shaft, and it apparently is missing the proximal epiphysis. Distally, it has two condyles and articulates well with the radius-ulna.

The ulna of *Typothorax* has never been described and is illustrated here for the first time (Fig. 7A-B). Proximally, it has a short, blunt olecranon process with a trihedral cross section. The olecranon fossa (notch) is shallow, concave and tapers distally. Its distal-anterior edge is a slightly convex, short articular surface

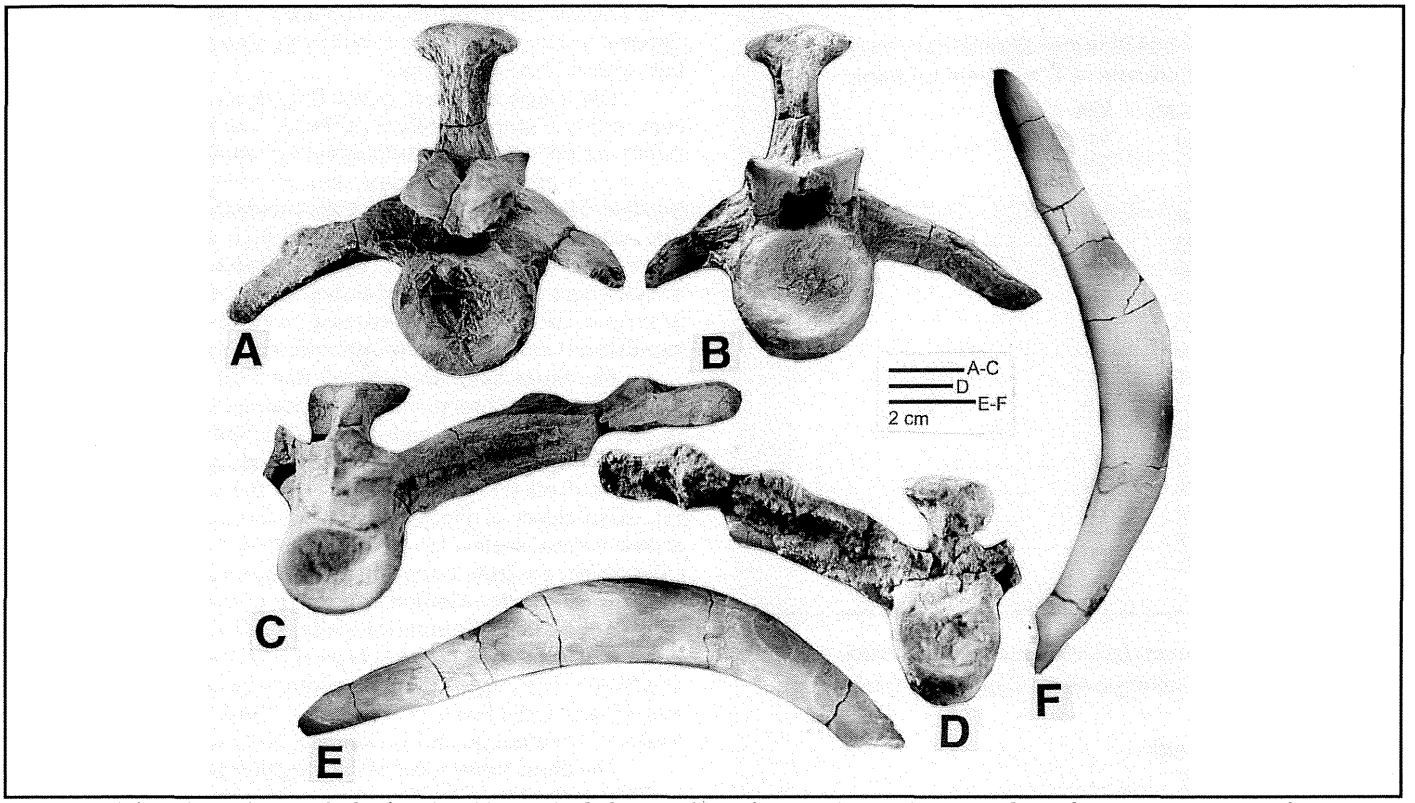

FIGURE 5. Selected vertebrae and rib of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-B**, Dorsal vertebra in **A**, posterior and **B**, anterior views. **C-D**, Caudal vertebra in **C**, anterior and **D**, posterior views. **E-F**, Rib.

for the proximal end of the radius. The shaft distal to that is laterally flattened and only flares slightly to the flat, slightly convex and roughened distal articular surface.

The radius of *Typothorax* also is described here for the first time (Fig. 7C-D). This slender bone has a broadly expanded proximal head with a concavo-convex saddle-like articulation for the humeral condyle. Its articular surface for the humerus is its flat postero-proximal end, and its antero-proximal face is convex. The shaft is nearly circular in cross section. It flares slightly distally to the nearly ovoid, distally convex and antero-posteriorly flattened distal head. The distal articular surface is nearly smooth.

A complete but slightly crushed left femur is present (Fig. 8A-C). This bone has the typical s-shaped flexure of many archosaur femora. In most features it is identical to the femora of *Typothorax coccinarum* illustrated by Long and Murry (1995, fig. 110), except for the more prominent distal condyles of *T. antiquum*. *T. antiquum* also appears to lack the well developed medial condyles of *T. coccinarum*.

The complete and slightly crushed left tibia of *T. antiquum* (Fig. 8D-E) also is nearly identical to those of *T. coccinarum* illus-

TABLE 5. Measurements (in mm) of the pelvis of NMMNH P-36075, the holotype of *T. antiquum*.

length (antero-posterior) iliac blade	125
length acetabulum	57
maximum width iliac blade	98
dorso-ventral diameter of the acetabulum	45
length sacral centrum 1	49
max diameter anterior surface sacral 1	46
length sacral centrum 2	46
maximum diameter posterior suface sacral 2	36
length ischia along midline of fusion	77
maxium width across ischia	130

TABLE 6. Measurements (in mm) of the limb bones of NMMNH P-36075, the holotype of *T. antiquum*.

Humerus
- Maximum length: 106
- Maximum proximal width: 42
- Maximum distal width: 37
- Mid-shaft diameter: 21

Ulna
- Maximum length: 114
- Maximum proximal width: 17
- Maximum distal width: 21
- Maximum length olecranon notch: 20

Radius
- Maximum length: 91
- Maximum proximal width: 23
- Maximum distal width: 17
- Mid-shaft diameter: 9

Femur
- Maximum length: 190
- Maximum proximal width: 57
- Maximum distal width: 66
- Mid-shaft diameter: 22

Tibia
- Maximum length: 109
- Maximum proximal width: 49
- Maximum distal width: 33
- Mid-shaft diameter: 19

Fibula
- Maximum length: 115
- Maximum proximal width: 29
- Maximum distal width: 32
- Mid-shaft diameter: 24

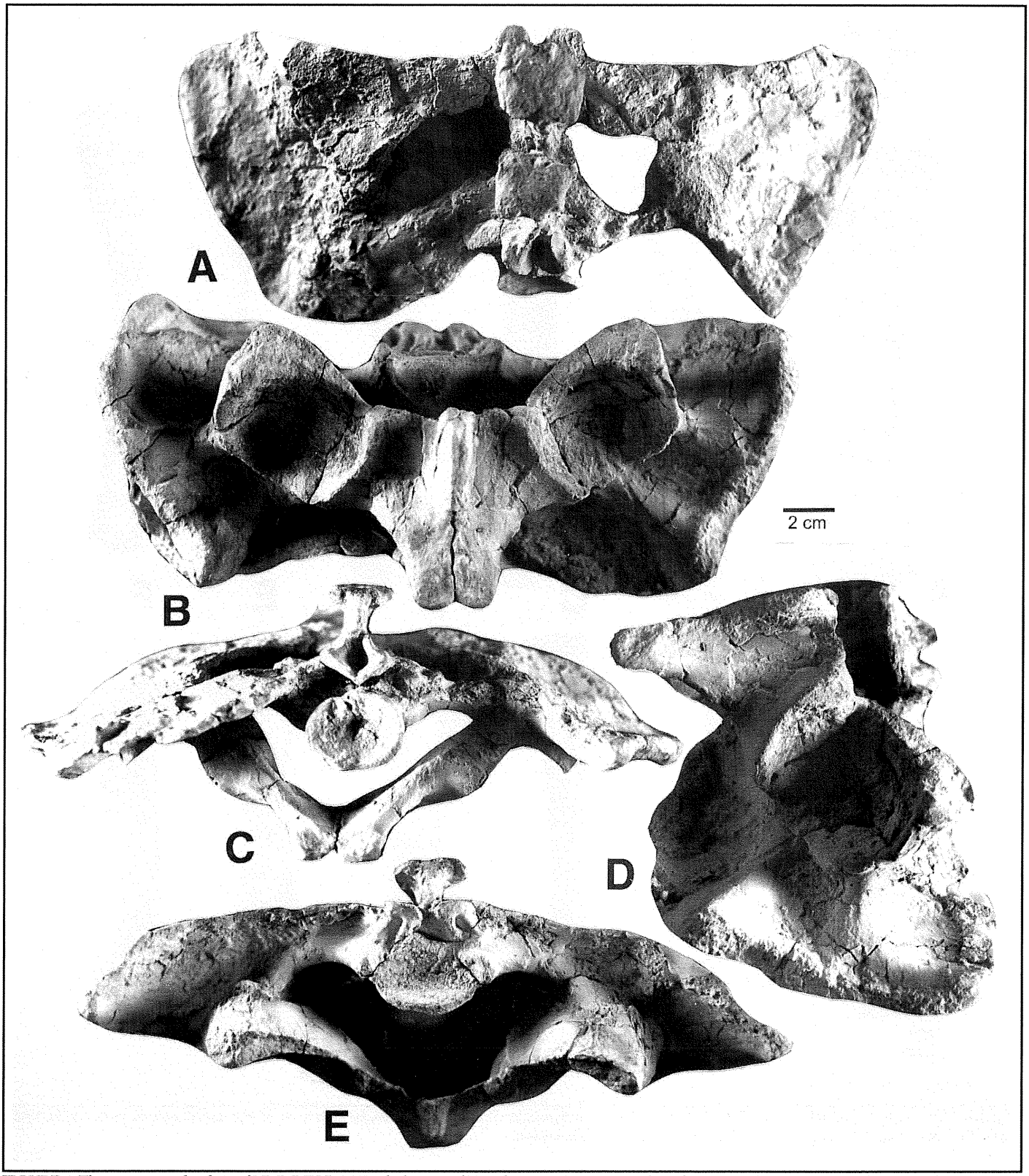

FIGURE 6. The sacrum and pelvis of NMMNH P-36075, holotype of *Typothorax antiquum* in **A**, dorsal, **B**, ventral, **C**, anterior, **D**, lateral and **E**, posterior views.

trated by Long and Murry (1995, fig. 111). The only difference seems to be the relatively narrower proximal end of the tibia of *T. antiquum*. While still robust, the tibia is clearly more gracile in *T. antiquum* than in *T. coccinarum*.

The complete left fibula (Fig. 8F-G) illustrated here represents the first time this bone has been described in *Typothorax*. It is very similar to the fibula of *Stagonolepis robertsoni* (Walker, 1961, fig. 19c-d), and thus can be described as a typical aetosaur fibula. The proximal end is an oval (in cross section) and slightly convex articular head that tapers to a straight proximal portion of the

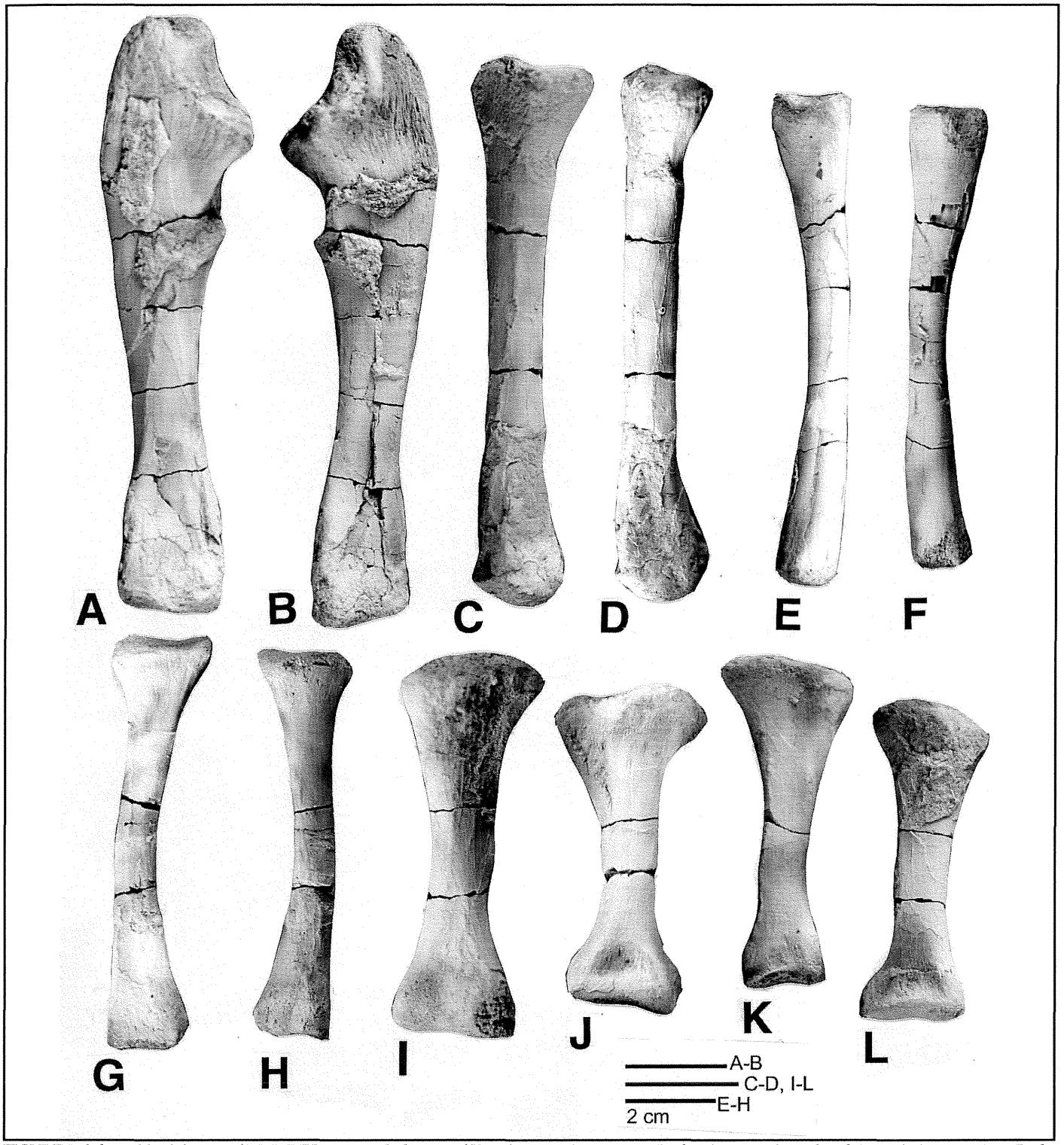

FIGURE 7. Selected limb bones of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-B**, Right ulna in **A**, lateral and **B**, medial views. **C-D**, Right radius in **C**, lateral and **D**, medial views. **E-L**, Metapodials and phalanges.

shaft. This head is inclined medially so that it overhangs the shaft medially. A large lateral trochanter (anterolateral process) forms a blunt flange and is located midway along the shaft. Away from that trochanter, the shaft has a nearly oval cross-section, being flattened anteriorly and posteriorly. The shaft distally broadens to a convex, transversely broad, roughened distal articular end.

Parts of the right and left pes are preserved, including the right and left calcaneum and astragalus, a total of five metatarsals from both sides, and four phalanges (Figs. 7E-L, 8H-K, 9). The calcaneum and astragalus (Fig. 9) form what has been traditionally called a "crocodile-normal" ankle in which there is a ball on the astragalus that articulates with a socket on the calcaneum (e.g., Parrish, 1986). The calcaneum of *T. antiquum* is a dorso-ventrally compressed bone that does not differ significantly from previously illustrated calcanea of *T. coccinarum* (Parrish, 1986, fig. 28; Long and Murry, 1995, fig. 112). The distal end is a broad and

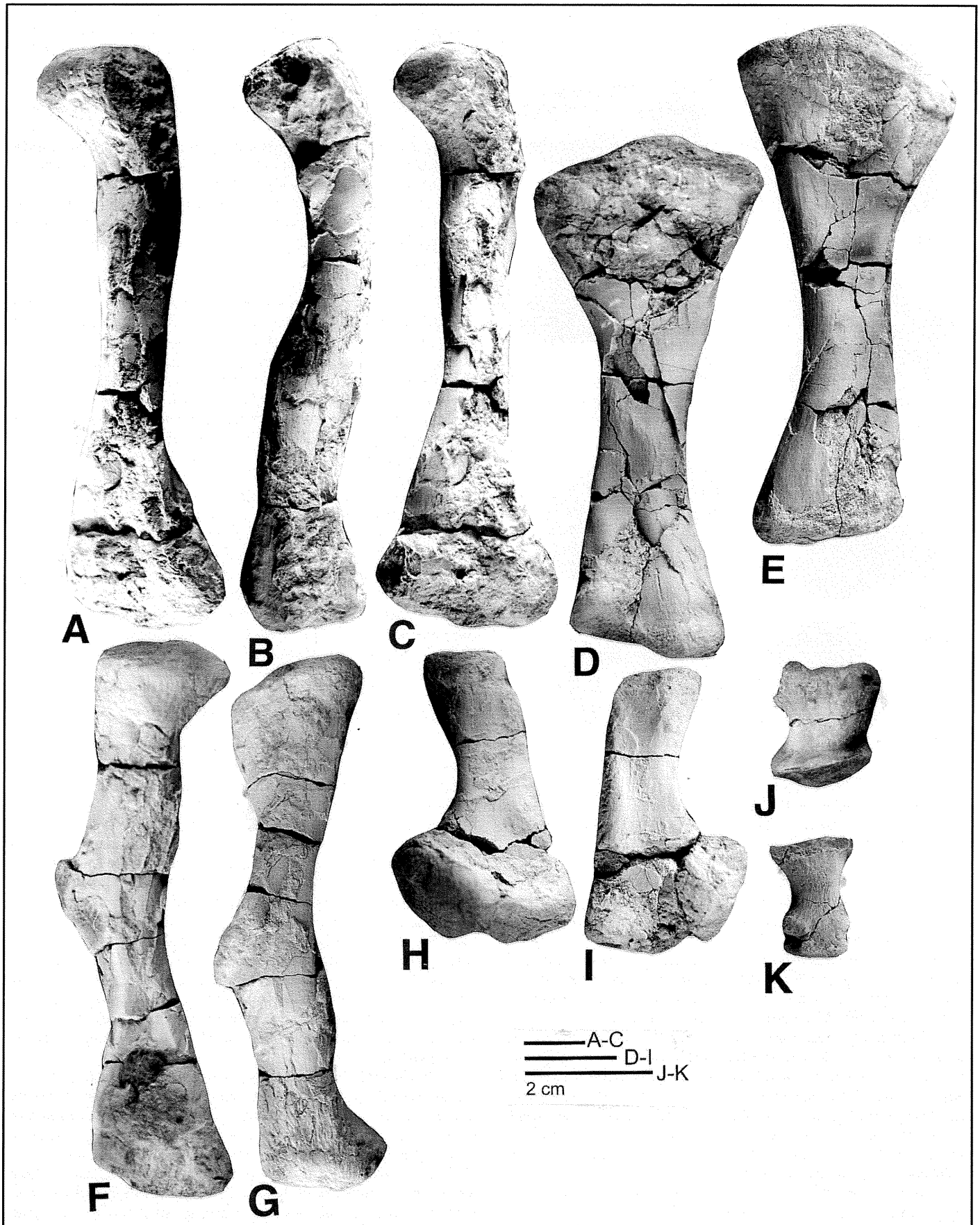

FIGURE 8. Selected limb bones of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-C**, Right femur in **A**, posterior, **B**, medial, and **C**, lateral views. **D-E**, Right tibia in **D**, medial and **E**, lateral views. **F-G**, Right fibula in **F**, medial and **G**, lateral views. **H-I**, Metatarsal V in **H**, lateral and **I**, medial views. **J-K**, Pedal phalanges in dorsal view.

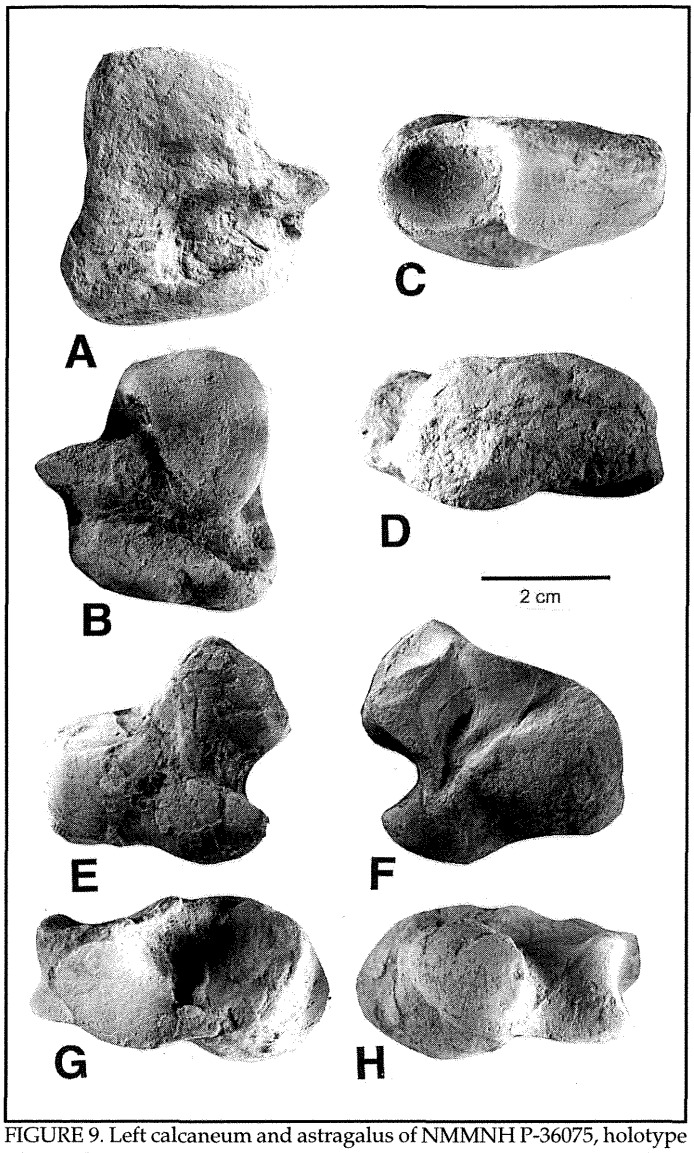

FIGURE 9. Left calcaneum and astragalus of NMMNH P-36075, holotype of *Typothorax antiquum*. **A-D**, Calcaneum in **A**, dorsal, **B**, ventral, **C**, proximal, and **D**, distal views. **E-F**, Astragalus in **E**, anterior **F**, posterior, **G**, proximal and **H**, distal views.

convex surface separated from the tuber by concave constrictions on the dorsal and ventral surfaces. There is a distinct convex ridge on the ventro-lateral margin of the calcaneum (cf. Long and Murry, 1995, p. 105). The tuber is a blunt flange with a broadly convex dorsal surface and a nearly flat ventral surface. The articular surface for the astragalus is a nearly v-shaped, concave surface medial to the tuber. Measurements of the calcaneum (in mm) are: length = 45, width distal end = 41, width tuber = 26.

Apparently, only Parrish (1986, fig. 28) has illustrated the atragalus of *T. coccinarum*, and that of *T. antiquum* is very similar. In anterior or posterior view this bone has a broadly trapezoidal shape. Proximally, it has a large, concave facet for the tibia medially and a smaller, concave facet for the fibula laterally. The distal end is broad and convex medially and has a convex facet for articulation with the calcaneum that projects laterally. Measurements of the astragalus (in mm) are: length = 39, width = 41.

Metapodials preserved with the holotype of *T. antiquum* range from elongate, rod-like elements (Fig. 7E-F) to shorter, robust elements with broad articular surfaces (Fig. 7I-L). Unfortunately, they were found disarticulated, and any association they once had is now lost, so we are unwilling to assign most of them to a particular limb or anatomical position. The more gracile metapodials (Fig. 7E-H) are nearly as long as the ulna and radius, a feature that is extremely unusual among aetosaurs.

The one diagnostic metapodial is the left (?) fifth metatarsal (Fig. 8H-I). As is typical of aetosaurs and many other archosaurs, this metatarsal is "hooked," with a broad, dorso-posteriorly directed articular surface proximally and a narrower distal articulation (Parrish, 1986, 1994), so that the element is L-shaped in lateral or medial views (Fig 8H-I).

The phalanges (e.g., Fig. 8J-K) are short and relatively robust. They are typical of aetosaurs in that they are dorso-ventrally compressed with broad articular surfaces and slight constrictions along their short shafts.

Discussion: *Typothorax* has long been diagnosed by its very broad dorsal paramedian scutes (width:length > 4:1) with ornamentation consisting of an essentially random distribution of pits and a prominent ventral keel that extends across the entire width of the scute (Long and Ballew, 1985; Heckert and Lucas, 1999). The lateral scutes are characteristically acutely folded into a laterally-directed wedge or spike (Long and Murry, 1995). The genus has generally been considered monospecific, represented only by its type species, *T. coccinarum* Cope, 1875 (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999, 2000, 2002a).

The specimens from the Santa Rosa and Garita Creek formations described here all display features that distinguish them from *T. coccinarum*, so they are assigned to *T. antiquum*. Particularly diagnostic are the relatively narrow dorsal paramedian scutes, but other features that clearly distinguish *T. antiquum* from *T. coccinarum* include the coarser and denser pitting on the paramedian scutes and the much more developed ridge on the lateral scutes. In spite of these differences, the Garita Creek and Santa Rosa specimens are more similar to *Typothorax* than any other named aetosaur. We are therefore certain that they represent a new species of *Typothorax* and are not a new genus.

TYPOTHORAX FROM THE TRUJILLO FORMATION

Specimens of *Typothorax* from the Trujillo Formation in east-central New Mexico are: NMMNH P-17135 (Fig. 10D), incomplete left paramedian scute from locality 505; P-17399 (Fig. 10B-C), incomplete paramedian scute from locality 504; P-17598, two paramedian scutes fragments from locality 554; and P-25628, one paramedian scute fragment from locality 2731. These specimens show diagnostic features (see above) of *T. coccinarum*, to which they are assigned. Thus, they have wide plate ratios and relatively dense, small pits. In particular, the pitting of both P-17135 and P-17399 is denser and smaller than that of a typical scute of *T. antiquum* (compare Fig. 10C-D to Fig. 10A). There is some variation of this character within the carapace of *T. coccinarum*, as one of us (ABH) has observed on UCMP specimens from the Canjilon quarry (see Long and Murry, 1995, for a complete listing). Still, dorsal paramedian scutes of *T. antiquum* do not ever possess the same fine pitting seen in at least some scutes of *T. coccinarum*, including the scutes illustrated here.

Hunt (1991, 2001a,b) also discussed MDM specimens of *Typothorax coccinarum* from the Trujillo Formation. Furthermore, it is apparent that at least some scutes of *Typothorax* are known from the Sonsela Member of the Petrified Forest Formation in Petrified Forest National Park (Heckert and Lucas, 2002b; Hunt et al., 2002), although we have not examined the Sonsela scutes in detail and cannot ascertain to which species of *Typothorax* they pertain. These fossils, and the presence of *Pseudopalatus*-grade phytosaurs, indicate the Trujillo Formation is of Revueltian age (Lucas, 1993; Hunt, 2001a). These records are the stratigraphically

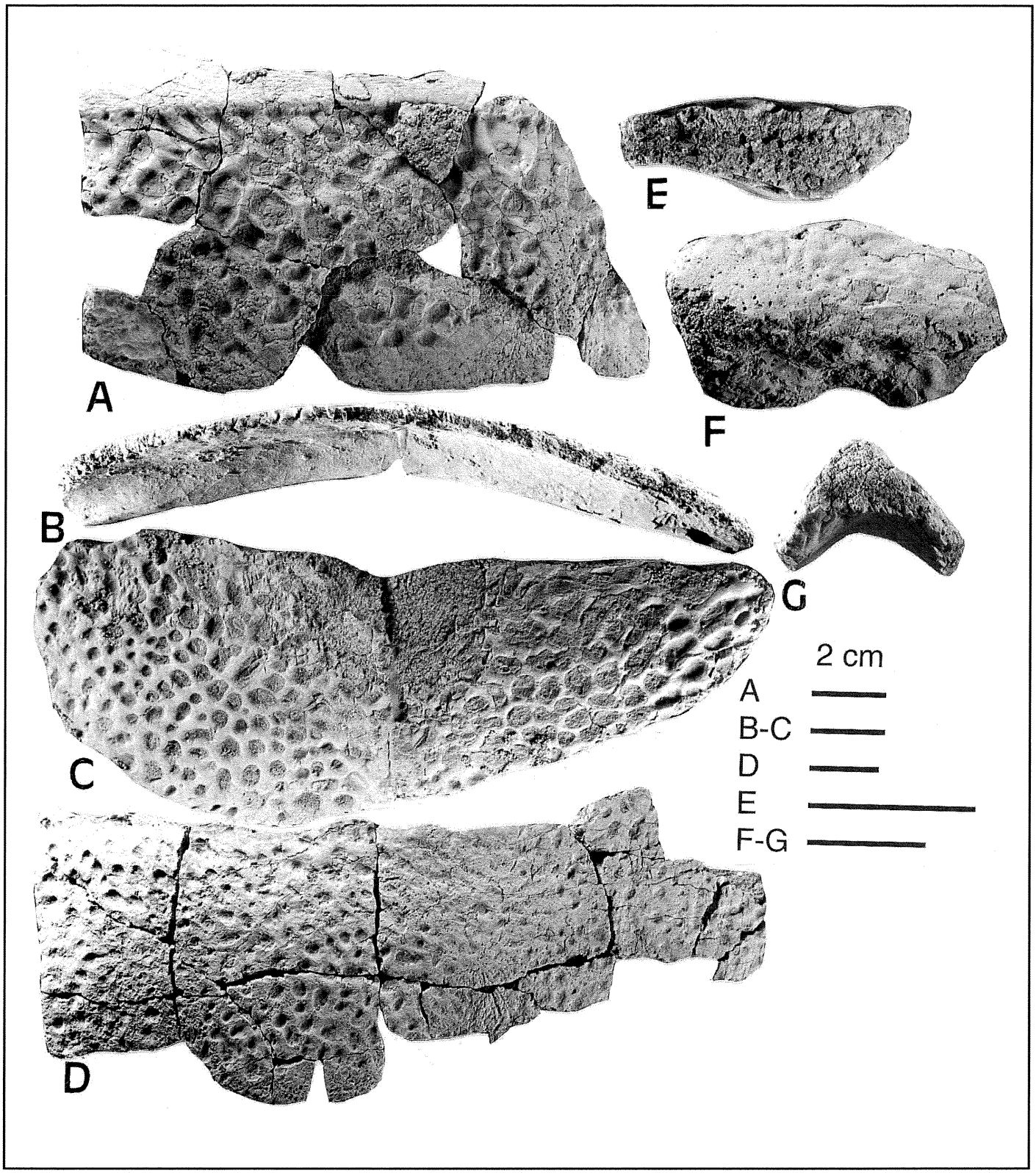

FIGURE 10. *Typothorax antiquum* from the Garita Creek Formation (**A**, **E-G**) and *T. coccinarum* from the Trujillo Formation (**B-D**) in east-central New Mexico. **A**, NMMNH P-17880, incomplete left paramedian plate from locality 1178. **B-C**, P-17399, incomplete right paramedian plate, in **B**, posterior and **C**, dorsal views, from locality 504. **D**, P-17135, incomplete left paramedian plate, dorsal view, from locality 505. **E**, P-17569, incomplete paramedian scute in cross sectional view from locality 413. **F-G**, P-17579, incomplete lateral scute in **F**, dorsal and **G**, cross sectional views, from locality 404.

lowest occurrence of *T. coccinarum* and are important because they confirm a Revueltian (Norian) age for the Trujillo Formation and the Sonsela Member, both of which have sparse tetrapod records.

BIOCHRONOLOGY

Recognition of *Typothorax antiquum* identifies two, temporally successive species of *Typothorax* in the Chinle Group. *T.*

antiquum occurs in strata of Adamanian age, whereas *T. coccinarum* is from Revueltian-age strata. Lucas (1998) identified *Typothorax* as an index fossil of the Revueltian lvf. This should be modified; *T. coccinarum* is an index fossil of Revueltian time.

Based on the correlation of Chinle Group strata presented by Lucas (1993, 1997), *Typothorax* has older records in east-central New Mexico than it does in eastern Arizona (Fig. 3). Thus, Lucas (1993, 1997) correlated the Sonsela Member of the Petrified Forest Formation in Arizona to the Trujillo Formation in east-central New Mexico, and assigned both an early Revueltian age. The presence of *T. coccinarum* in the Trujillo Formation is consistent with this correlation. However, note that *Typothorax* has not previously been reported from the largely unfossiliferous Sonsela Member, although Hunt et al. (2002) note that some specimens of *Typothorax* reported by Long and Murry (1995) from the Petrified Forest National Park were probably derived from the Sonsela, specifically the "Camp Wash zone" of Roadifer (1966) (see also Heckert and Lucas, 2002). Unfortunately, we have not been able to examine these fossils and determine which species of *Typothorax* these fossils (mostly isolated scutes) represent.

EVOLUTION

In spite of the relative abundance of aetosaur scutes in the Chinle Group (Long and Ballew, 1985) and locally abundant aetosaurs elsewhere (e.g., O. Fraas, 1877; E. Fraas, 1896; Walker, 1961), aetosaur evolution is poorly understood (Heckert and Lucas, 2000). This is in large part because many taxa are known from relatively fragmentary fossils, and complete skulls and skeletons are both extremely rare. This is almost certainly because aetosaurs were highly terrestrial animals, and thus not nearly as likely to be preserved as contemporaneous aquatic taxa of similar size such as phytosaurs and metoposaurs.

Regardless of these difficulties, we and other workers have attempted cladistic analyses of aetosaurian interrelationships (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 2000). These analyses, like non-cladistic analyses before them (Walker, 1961; Krebs, 1976), indicate that *Typothorax* is one of the most derived aetosaurs. However, it is also closely related to some of the earliest aetosaurs, including *Longosuchus* and *Desmatosuchus*. Thus, the Revueltian (early-mid Norian) *T. coccinarum* appeared to have a significant ghost lineage dating back to Otischalkian (early-late Carnian) time (e.g., Heckert and Lucas, 2000, fig. 9). The presence of *T. antiquum* in strata of Adamanian (Carnian) age substantially shortens the length of this "ghost lineage" (Fig. 11).

Typothorax antiquum also provides insight into the evolution of the genus as a whole. Not only does *T. antiquum* appear first in the stratigraphic record, but it also possesses several more primitive characteristics than *T. coccinarum*, including the narrower dorsal paramedian scutes and most features of the ilium. Importantly, these features are considered primitive by all students of aetosaurs, whether utilizing cladistic (Parrish, 1994; Heckert and Lucas, 2000) or non-cladistic (Walker, 1961; Long and Murry, 1995) methods.

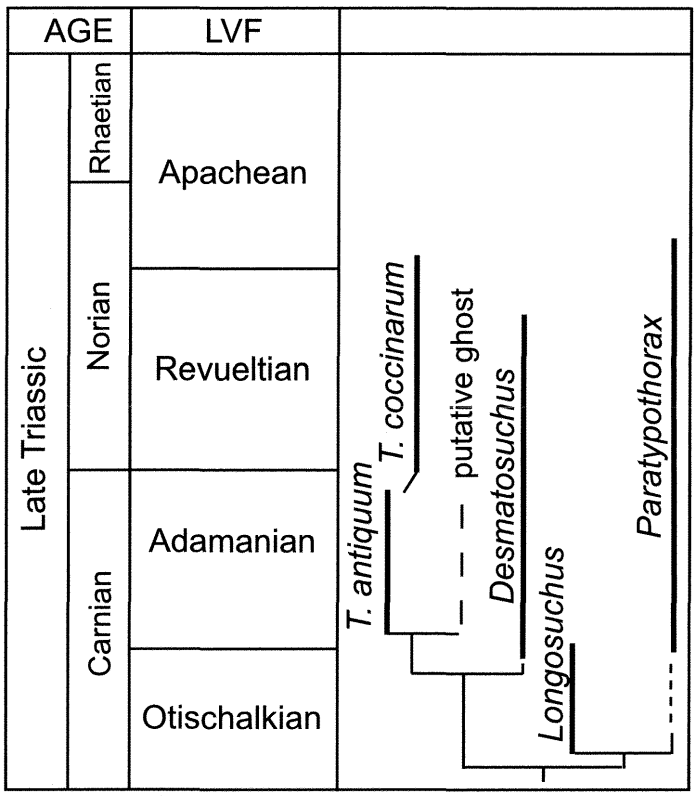

FIGURE 11. Evolutionary tree of desmatosuchine aetosaurs showing the apparent phyletic relationship of *T. antiquum* and *T. coccinarum*. Other phylogenetic relationships follow Heckert and Lucas (2000).

The most parsimonious explanation of this pattern is that *T. antiquum* and *T. coccinarum* are an anagenetic species pair, with the younger and more advanced *T. coccinarum* derived from the older and more primitive *T. antiquum* (Fig. 11). An alternative, cladogenetic hypothesis requires that, in spite of the occurrence of *T. antiquum*, an additional sister taxon of *T. coccinarum* (or *T. coccinarum* itself) must be present throughout much of Otischalkian and Adamanian time. Consequently, we embrace an anagenetic model where *T. antiquum* evolves phyletically (*sensu* Simpson, 1944), with *T. coccinarum* appearing at the onset of Revueltian time as a result of this evolution.

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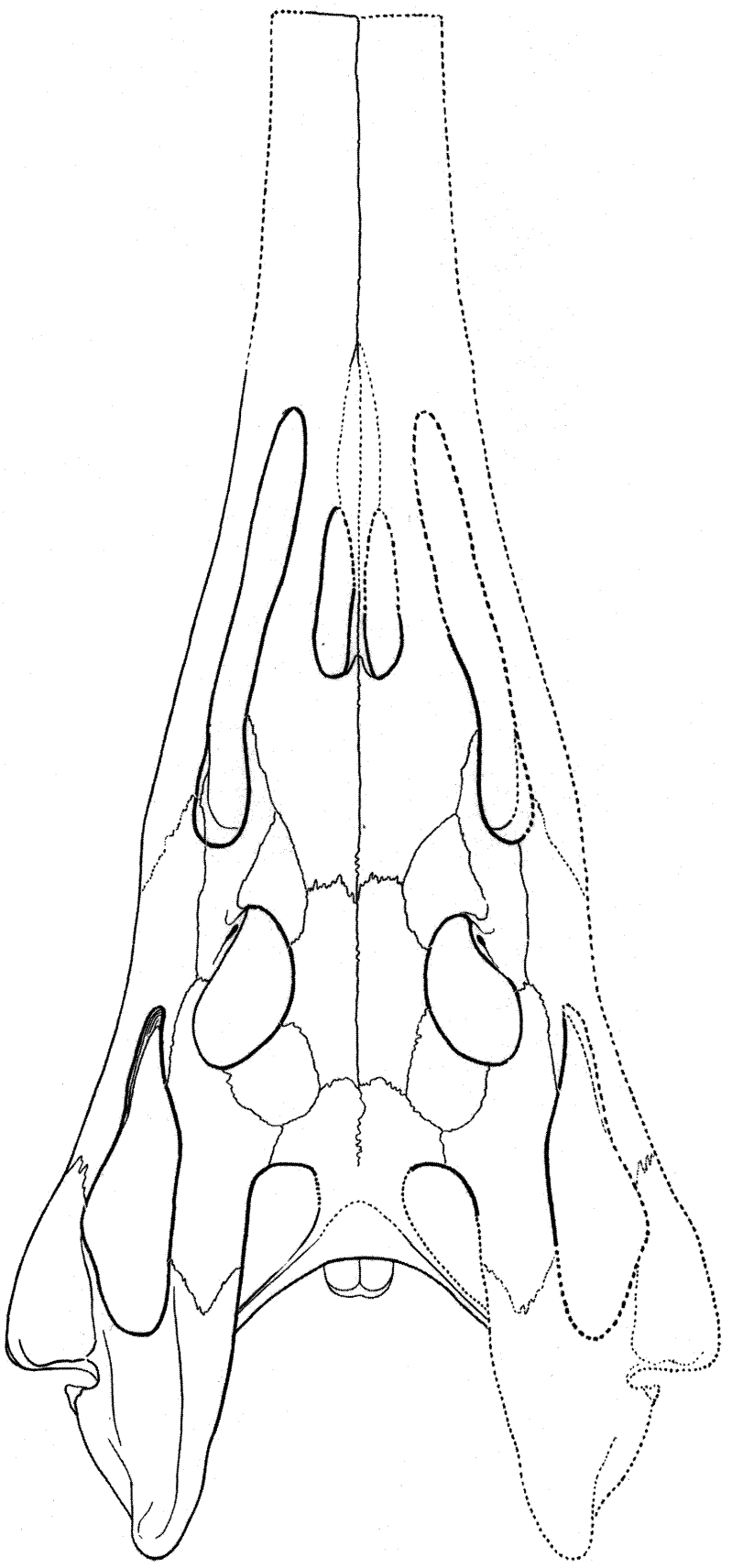

Skull of *M. zunii*, 7307/27159, dorsal view, x1/3 (from Camp, 1930, fig. 9, p. 35).